The Tidal Migration of *Donax variabilis* Say

(Mollusca : Bivalvia)

BY

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(2 Text figures)

INTRODUCTION

THE BEACH CLAM, *Donax variabilis* Say, 1822 is a bivalve that inhabits the intertidal zone of sandy beaches, ranging from Texas around the tip of Florida to the shores of the Carolinas (ABBOTT, 1954). These clams have the ability to maintain large populations of individuals on wave-swept beaches because of their morphological and behavioral adaptations to this environment.

Donax variabilis, commonly called the coquina, exhibits a stereotyped migration pattern in that it moves shoreward and seaward with the flood and ebb tides. Previous investigators have dwelled mainly upon the mechanism of this tidal migration, and many hypotheses have been suggested to account for it in this and other species.

Investigations of migration patterns were carried out by MORI (1938, 1950) on *Donax semigranosis* Dunker, 1877, in Japan. He proposed an "internal time clock" mechanism to be responsible for the migrational behavior. HEDGPETH in 1953, however, was the first to publish observations and theories concerning the tidal migration of *D. variabilis.* COE (1955) and POHLO (1967) confined their studies to the general ecology of *D. gouldii* Dall, 1921, on the coast of California and Western Mexico. JACOBSON (1955) observed *D. fossor* Say, 1823 on Long Island, New York. LOESCH (1957) in his studies on the ecology of two species of *Donax* in Texas also mentioned the migration activity. TURNER & BELDING (1957) hypothesized that the acoustic shock of waves breaking on the beaches initiates shoreward migration, and the seaward migration may be due to a "trigger and memory" mechanism which is activated at the changing of the tides. In 1959 EDGREN observed *D. variabilis* at Clearwater Beach, Florida, and reported on the migrational activity. WADE (1964, 1965, 1967a, 1967b) observed several species of *Donax* in the West Indies and set forth his migrational theories which are based on the acoustic shock stimulation concept. He classified the different zones of sandy beaches into 4 major regions: surf, wash, spray, and coast. The wash zone was further divided into saturated and unsaturated areas. The former is always covered by a thin slick of water, thereby completely filling the interstitial sand spaces. Farther landward, the unsaturated wash zone is covered by water from breaking waves, but it has no interstitial water because of drainoff to the lower beach regions. The other zones are self-explanatory. In the present study, Wade's classification of zones is used when defining specific areas on the sandy beach.

Donax variabilis occur predominantly in the saturated wash zone of the beach (see Figure 1). It is in this area that they are able to burrow due to the unpacked quality of the sand. In the unsaturated wash zone, the sand is

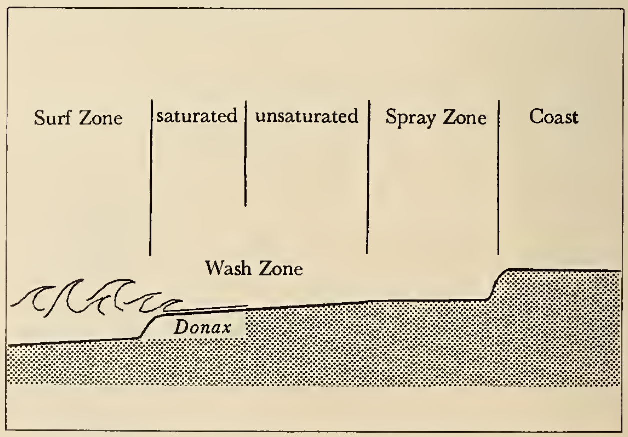

Figure 1

Profile of a sandy beach (zonation nomenclature after WADE, 1967a) *Donax variabilis* population represented by light area marked *Donax.*

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packed too tightly, and in the surf zone the boiling waters continually disrupt the sand, affording no foothold.

Recently, ANSELL (1969), studying *Donax incarnatus* Sowerby, 1825 near Shertallai, India, comprehensively reviewed the existing literature on *Donax* migration.

One of the unifying facts of all previous observations is that *Donax* usually responds to acoustic shock by exhibiting a jumping response. The coquinas emerge from the sand in response to any sharp shock, such as those from breaking waves or a blow from a shovel. WADE (1965) placed *D. denticulatus* Linnaeus, 1758 in a bucket filled with water and sand and observed the jumping in response to a sharp blow on the side of the bucket. Upon draining the water, the clams were unable to respond because the overlying sand was packed.

MATERIALS AND METHODS

The specimens used in this study were observed and collected at 3 principal sites on the Gulf Coast of Florida: Alligator Point, Franklin County; Siesta Key Beach, Sarasota County; Panama City, Bay County (Figure 2).

The interrupted line transect method of sampling described by WADE (1965) was used to determine the pattern of zonation in *Donax variabilis*. A line was laid down across the beach from the surf to the upper limits of the sand, and comparative samples were taken at 20 cm intervals at right angles along this line.

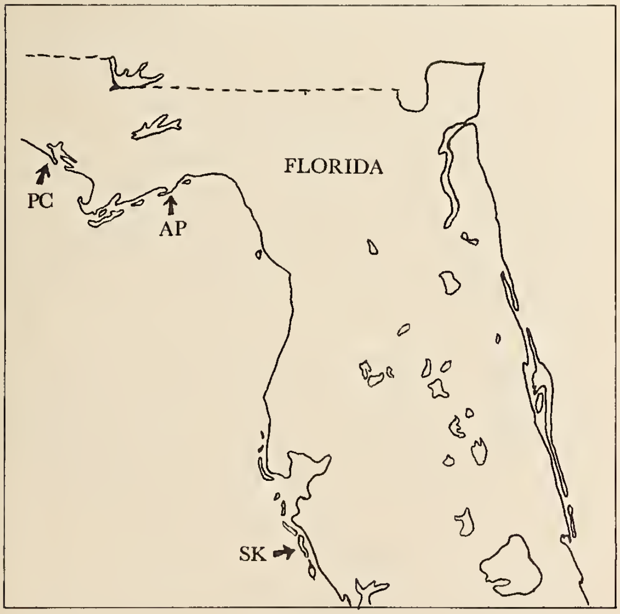

Figure 2

Collection sites of *Donax variabilis* in Florida
AP – Alligator Point; PC – Panama City;
SK – Siesta Key Beach

The sand bucket experiments of WADE (1965) were repeated at various phases of the tide to determine whether the jumping response was related to an intrinsic timing mechanism as well as to acoustic shock. The experiment was conducted with varying amounts of water in the bucket.

Observations were made on actively migrating clams to determine whether or not they follow any specific pattern of transport from one area to another. Live clams were observed as they were transported by the wash and while burrowing into the sand. Preserved specimens were placed among migrating individuals and were observed to determine whether or not the living clams are passively oriented to the flow of water.

The hypotheses of TURNER & BELDING (1957) and MORI (1938, 1950) were offered without experimental evidence. In order to test these hypotheses, I transported specimens of *Donax variabilis* from one site of collection to another and observed the resultant migratory behavior. The tides at the 3 principal collection sites are all different in nature. Those of Alligator Harbor are semi-diurnal. Panama City has a diurnal rhythm, and Sarasota experiences a mixed rhythm. The dates and tidal fluctuations are listed in Table 1.

Table 1

Times of High and Low Water at Collection Sites in Florida

	Alligator Point			
	Aug. 5, 1968	Aug. 6, 1968	Sept. 5, 1968	Sept. 9, 1968
high tide	0121	0209	0209	0327
low tide	0525	0637	0731	0955
high tide	1053	1209	1315	1603
low tide	1901	1955	2025	2213

	Siesta Key Beach, Sarasota	
	August 5, 1968	August 6, 1968
high tide	0834	0940
low tide	1808	1856

	Panama City	
	September 5, 1968	September 9, 1968
high tide	0841	0758
low tide	1958	2340

Approximately 5000 clams were transported from one collection site to another for each observation. The clams were taken from the sand, dried, and the valves were marked with black waterproof "Magic Marker." The clams were then wrapped in polyethylene bags and put into a styrofoam cooler containing ice. By reducing the metabolic activity in this manner, the clams could be transported without supplying them with oxygen. At the site of observation, the clams were removed from the bags and placed in sea water until they resumed normal siphoning (usually about 15 minutes). They were then placed in the upper limits of the saturated wash zone to resume their migratory activity.

Previous attempts to transport coquinas without cooling them resulted in a high mortality of individuals. However, those individuals that did survive the trips migrated with the indigenous clams (see Discussion), exactly as did the cooled clams.

OBSERVATIONS AND DISCUSSION

It was confirmed that acoustic shock is the cause of the jumping response exhibited by *Donax variabilis*. At all phases of the tide the specimens reacted when the bucket was struck. This was only true, however, if the bucket contained water above the level of the sand. When the water was drained, the clams no longer responded to the acoustic shock. This may be interpreted in two ways: either the sand was packed too tightly for the clams to emerge, or the interstitial water was not present to carry the shock wave to the clams. The latter possibility is the more probable of the two because the sand was not packed too tightly to prevent some of the clams from pushing to the surface (not a jumping response), when the water was drained. Similar emergence is also observed in nature, for if specimens are stranded in the unsaturated area of the wash zone, they may push themselves out of the substrate independent of any wave induced shock and may be carried seaward by the next downrush of water. This is in response to the water drainoff from the interstitial sand spaces and not to acoustic shock. In this case, the process of emergence is a gradual one, much different from the sudden jumping response exhibited when the clams are situated in saturated areas. The process of emergence is observed predominantly during ebbing tide. When the clams have reached their peak of ascent up the beach, the tide has already started to recede, moving the saturated wash zone seaward. Clams that were previously in saturated sand find themselves in unsaturated sand, and they emerge to the surface from which the wash of the waves carries them into saturated areas, thereby maintaining zonation within the saturated wash zone.

The antero-posterior axis of *Donax variabilis* is oriented perpendicularly to the shore line during seaward or shoreward migration. This orientation appears to be passive, for it is maintained in the case of the dead as well as the living clams. The dead clams, however, are completely at the mercy of the wash currents because they are not able to maintain zonation by burrowing. Eventually they are carried into the surf zone. A living clam, on the other hand, uses its muscular foot and protrusive siphons as effective braking devices. After being washed shoreward, living specimens extend the foot and siphons and begin to burrow into the sand at the onset of the backwash. This behavioral pattern is continued until the clams find themselves in unsaturated sand when the tide changes. At this time they respond to the drainage as described above. It must be remembered that the clams, even though they are in unsaturated sand, are still in the wash zone, and the shoreward extension of water from the breaking waves can effectively wash the clams seaward to the saturated area.

According to TURNER & BELDING (1957) *Donax variabilis* does not show specific zonation, nor do the individuals sort according to size. This is not the case with the coquinas at Sarasota, Panama City, or Alligator Point. Within the saturated wash zone a definite sorting pattern for size was observed. The smallest individuals are found at the top of the saturated wash zone (shoreward). The animals get progressively larger toward the sea. The largest individuals are found in the surf zone. I found that these clams are not able to maintain their zonation because they are inactive and near death, as evidenced by the deteriorated condition of the body tissues, so they are washed passively into the surf zone.

From the above observations, I conclude that the tidal migration of *Donax variabilis* is purely a phenomenon in which the animal responds to various physical stimuli in its environment independently of any endogenous mechanism, if indeed it even exists. However, the following study of tidal variation was undertaken to test the hypothesis.

On 5 August, 1968, clams were transported from Alligator Point to Siesta Key Beach, Sarasota. They were collected at 0545 when the tide was rising at Alligator Point. At 1130, while the tide in their normal environment was still rising, they were placed on the beach at Sarasota during an ebbing tide. Within a few minutes the clams had burrowed into the saturated wash zone. Over the next 3 hours they migrated seaward with the ebbing tide, along with the Sarasota population. Observations were suspended and again resumed at 1810. The Alligator Point population had become widely distributed laterally along the beach, but still maintained its position in the saturated wash zone with the indigenous clams. At this time the tide began to flood, and the clams started normal shoreward migration. The following day, Sarasota clams were transported to Alligator Point, leaving Sarasota at 1000 during flood tide, arriving at 1600 during ebb tide. The Sarasota clams, which normally would be experiencing a rising tide, began migratory behavior in response to the new tidal pattern.

The trips to Panama City involved less travel time than those to Sarasota and afforded more time to observe entire tidal fluctuations. On 5 September, 1968, at 0735, coquinas were collected at Alligator Point during flood tide and placed on the beach in Panama City at 0940 during ebb tide. The clams again migrated with the local individuals. At 1600, Panama City clams were transported to Alligator Point, arriving at 1815. The tide at both locations at this time was ebbing, and the clams migrated seaward. The final transplant of specimens was made on 9 September, 1968. Clams were collected from Panama City during flood tide at 0920 and carried to Alligator Point by 1250, also during flood tide. The clams from Panama City were observed throughout the next complete tidal change from high water at 1603 until low water at 2213. Night observations were made with the aid of lanterns and also indirectly by sampling the beach profile using the interrupted line transect method. The clams did not follow their original diurnal migratory pattern, but they migrated in accordance with the semidiurnal tide at Alligator Point.

Since the transported coquinas migrated immediately with the indigenous population without a period of adaptation, an endogenous rhythm is unlikely.

The experiments have shown that *Donax variabilis* responds to acoustic shock by jumping into the uprushing water. The clams respond to the shock only if they are situated in the saturated wash zone. It is postulated that the interstitial water in this area carries the acoustic shock to the animals. Clams carried up the beach to the unsaturated wash zone are usually washed back into the saturated area before they have a chance to burrow under the sand, or else they uncover themselves, withdrawing foot and siphons, thus loosening their hold on the substrate and allowing themselves to be carried seaward.

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